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The development of air chambers in the Ricciaceae

PAULINE E. HIRSH

The thallus in the family Ricciaceae is characterized by the presence of clearly defined air spaces, varying in different species in size and shape. On the basis of the structure of the tissues and enclosed air chambers a subdivision of the old genus *Riccia* into smaller genera is made by some writers. For example, Evans and Nichols in their "Bryophytes of Connecticut" have placed in the genus *Riccia* those species with air spaces in the form of narrow canals lying between rows of cells at right angles to the upper surface of the thallus. Species with the green tissue arranged in layers one cell thick, separating irregular air spaces from one another, they placed in the genera *Ricciella* and *Ricciocarpus*, the latter characterized by an epidermis with pores, the former by an epidermis without pores, though sometimes becoming ruptured irregularly with age.

In the Botanical Gazette for September, 1907, Barnes and Land published a paper dealing with the origin of air chambers in the Marchantiales. They studied representatives of as many groups as they could obtain, and described results so uniform as to make it, in their opinion, a matter of doubt whether any other mode of origin exists than that found in every plant investigated. They concluded that the "air chambers of Marchantiales arise invariably by the splitting of internal cell walls, usually at the junction of the outermost and first internal layer of cells." * In the Ricciaceae they examined only *Riccia fluitans* and *R. natans*. They stated that in these species "the origin of the air chambers is exactly alike, though the later course of development seems to be different. The origin of both is certainly by internal cleavage, and it is quite evident that the air chamber is wholly unrelated to the sex-organ pit." †

At the time that the present study was undertaken, the only fresh material available was "*Riccia lutescens*," the terrestrial form of *Ricciocarpus natans*, which was obtained from the marshes near the southern end of Cayuga Lake. In addition, material of *Riccia Frostii* Aust., which had been preserved in alcohol, was used.* For comparative purposes herbarium material of *Riccia nigrella*, *R. glauca*, *R. Miyakeana*. *R. crystallina*, *R. arvensis hirta*, *R. fluitans*, *R. Donnellii*, and *Ricciocarpus natans* was studied. This was prepared for sectioning by first soaking it in dilute KOH and warm water before running it through the alcohols and cedar oil, and imbedding finally in paraffin. Although the tissue of this herbarium material was distorted and could not be used as a basis for positive statements or drawings, it was evident that the first three species named presented a different type of air chamber from that found in the two species studied by Barnes and Land; and the earliest stages suggested an entirely different origin. *Riccia Frostii* Aust. also exhibited the same type of air chamber; and as this had been preserved in alcohol the tissue was in good condition, so that satisfactory sections through the apical region could be obtained and the development of the air chambers could be followed with certainty.

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* Barnes and Land. Bot. Gaz. 44: 213. 1907.

† Barnes and Land. *L. c.* 205.

A study of *Ricciocarpus natans* showed that in every instance the air spaces arise through cleavage. The figures (1–3 inclusive), made from sections close to the growing point, display this clearly. There is no doubt concerning the origin of space A in FIGURE 1. B and C in the same figure show older spaces that have opened out to the surface FIGURE 3, A, indicates cell division preparatory

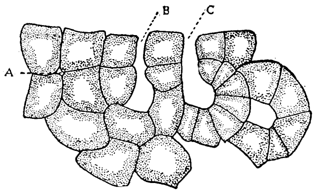

FIGURE 1. *Ricciocarpus natans*. Vertical longitudinal section of thallus near the growing point. *A*, early stage of an air chamber; *B* and *C*, older chambers which have opened to the outside.

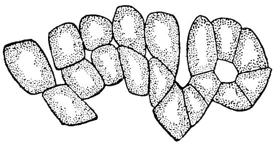

FIGURE 2. *Ricciocarpus natans*. Section nearly parallel to the surface showing origin of air chambers.

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* The material was collected near the "Kaw River," Kansas, by an unknown collector. The writer is indebted to Professor Alexander W. Evans for its determination.

to the closing of the air chamber C that has broken out to the surface. All of the figures confirm the truth of the statements of Barnes and Land; and they cannot be interpreted in any other way than in consonance with their observations.

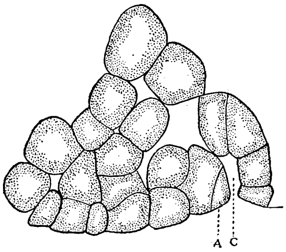

FIGURE 3. *Ricciocarpus natans*. *A*, cell division preparatory to closing the chamber *C*.

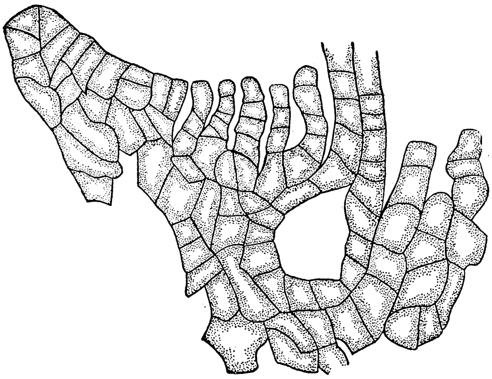

FIGURE 4. *Riccia Frostii*. Vertical longitudinal section, showing archegonium and origin of chambers and filaments.

An examination of *Riccia Frostii* Aust., however, indicates an entirely different structure. FIGURES 4, 5, and 6 present a condition strikingly in contrast with that shown in the previous figures of *Ricciocarpus natans*. In FIGURE 6, A is the apical cell; M is a young archegonium; B, C, and D, are tiny depressions lying between the rounded ends of the outermost layer of cells; N and O show older spaces, and at P is shown the way in which the elongated, narrow air spaces are closed at the end. The air chambers of *Riccia Frostii* Aust. are, therefore, narrow chambers or canals, which are the spaces between the elongated filaments or rows of cells at right angles to the upper surface of the thallus. FIGURE 6 shows clearly the way in which these filaments and spaces originate. Immediately back of the apical cell, the superficial cells arch outward in a papillate manner as a result of the cessation of growth at the lines of their junction. As they elongate they are divided by transverse walls so that filaments or rows of cells are formed, which are separate and distinct from one another. The intervening spaces in this species are formed, therefore, not by the cleavage or the separation of mature tissues, but in a manner almost exactly indicated by the diagrammatic scheme given by Barnes and Land in their figure 1. During the formation of the filaments there is a marked growth in the thallus in which the protruding filaments do not share, so that the air spaces broaden perceptibly. In the older parts of the thallus the air spaces may become nearly completely closed (FIGURE 6, P) through the enlargement of the terminal cells of the filaments; but, nevertheless, they retain their canalicular form and present an entirely different appearance from the irregular but more or less polygonal air spaces of *Ricciocarpus natans.*

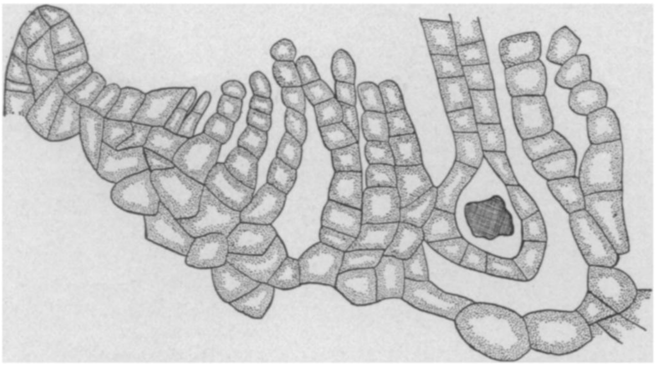

FIGURE 5. *Riccia Frostii.* Later stage, showing similar structures.

This method of development is clearly in harmony with Leitgeb's account of the origin of intercellular spaces. In his "Untersuchungen über die Lebermoose" Leitgeb maintains that near the growing point on the dorsal surface there appear between four cells small pits that in profile view are simply dark points, "that these impressions arise not by cleavage but in this way, — that the free outer walls of the enclosing cells grow up over these places." B, C, and D in FIGURE 6 are without doubt these pits. He states further that there is a possibility that occasionally these depressions could elongate through a splitting from without in; but he rejects this in favor of the view that their increase in size is accomplished by a growth in thickness of the thallus dorsally.* He thus believed that the sex organs are visible at the same time as the pits that form the very beginning of the intercellular space formation, and that, as in the case of the former, the whole cell becomes imbedded by an upward growth of the surrounding tissue, so in the case of the latter the bottom of the pit becomes sunken in the thallus by similar growth.

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* Leitgeb, Untersuchungen über die Lebermoose 4: 17, 27. 1879.

From what has been said it is evident that there are two methods of origin of the air spaces in the Ricciaceae : the first, by internal cleavage, resulting in the formation of broad, irregular, chamber-like spaces separated by plates of green cells one layer thick; the second by the upward growth of filaments at right angles to the surface of the thallus, resulting in the formation of elongated, narrow air chambers. The two species studied by Barnes and Land represent only *Ricciella* and *Ricciocarpus*, in which groups the origin of the air chamber is by internal cleavage. *R. Frostii* Aust., on the other hand, is a true *Riccia*, in which the air chambers are formed by the growth of filaments at right angles to the surface.

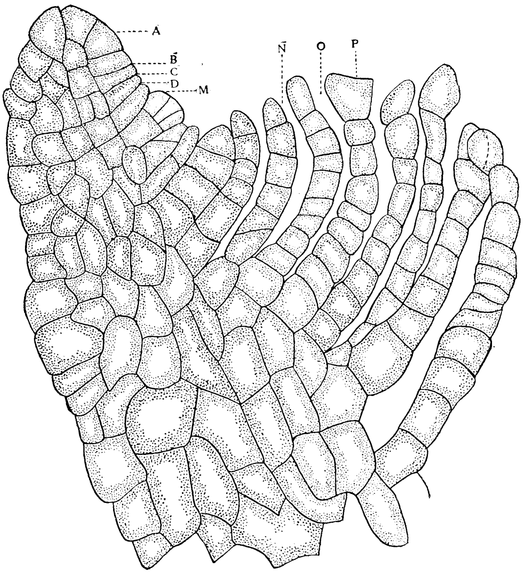

FIGURE 6. *Riccia Frostii.* *A*, apical cell; *M*, young archegonium; *B*, *C*, and *D*, tiny depressions formed by the beginning outgrowths of cells ; *N* and *O*, older air chambers between filaments ; *P*, terminal cell of filaments swollen until chambers are partly closed.

This work was done in the botanical laboratory of Cornell University at the suggestion and under the supervision of Dr. E. J. Durand.